OBSERVATIONS ON INSTALLMENT EGG HATCHING IN THE BROWN SALTMARSH MOSQUITO, *AEDES CANTATOR*

THEODORE G. ANDREADIS

Department of Entomology, The Connecticut Agricultural Experiment Station, P. O. Box 1106, New Haven, CT 06504

ABSTRACT. Field collected, first generation female *Aedes cantator* were shown to produce heterogeneous eggs that exhibit variable hatch in response to serial inundations and cold conditioning in the laboratory. Nearly 85% of the egg batches exhibited some hatch with the first flooding, representing 69.4% of the total overall hatch. However, 56% of the same egg batches displayed further hatch with subsequent floodings and 34% showed partial hatch before and after cold conditioning. The significance of these findings is discussed in relation to the biology of *Ae. cantator.*

Partial hatch of viable mosquito eggs in response to suitable stimuli from one inundation to the next is commonly referred to as "installment hatching" (Gillett 1955a, Mallack et al. 1964, Breeland and Pickard 1967). It is a reproductive strategy that has obvious advantages for long-term survival of species that develop in temporary bodies of water that are subject to irregular fluctuations. The phenomenon appears to be prevalent among multivoltine floodwater species of *Aedes* and *Psorophora* which have facultative egg diapause (e.g., *Aedes vexans* (Meigen) and *Psorophora confinnis* (Lynch Arribalzaga)) (Gjullin et al. 1950, Travis 1953, Mallack et al. 1964, Breeland et al. 1965, Moore and Bickley 1966, Breeland and Pickard 1967, Woodard et al. 1968, Wilson and Horsfall 1970, Becker 1989) and has also been observed in *Aedes aegypti* (Linn.) and *Aedes africanus* (Theobald) (Gillett 1955a, 1955b).

Although installment hatching is widespread, hatching behavior varies greatly among species. For example, Travis (1953) has shown when eggs of *Aedes sollicitans* (Walker), *Aedes taeniorhynchus* (Wied.), and *Ps. confinnis* are repeatedly flooded and dried, they continue to hatch through the third, fifth and seventh floodings, respectively. However, most eggs of *Ae. sollicitans* (62.8%) will hatch with the first flooding whereas the greatest percentage of *Ae. taeniorhynchus* (84.3%) and *Ps. confinnis* (71.4%) eggs will not hatch until the third flooding.

Variation in hatching response can also occur within populations of the same species and among eggs laid by the same female (Gillett 1955a, 1955b; Moore and Bickley 1966; Becker 1989). This variation is believed to have an inherited basis that is determined by factors contributed by both parents (Gillett 1955b).

While conducting a study on vertical transmission of a microsporidian parasite, *Amblyospora connecticus* Andreadis, in the brown saltmarsh mosquito, *Aedes cantator* (Coq.), it became necessary to obtain individual egg batches from wild caught females and subject these eggs to alternating periods of flooding and drying. During the course of this study, distinct patterns of installment hatching were observed in uninfected egg batches. These observations are reported herein and discussed in relation to the biology of *Ae. cantator.*

Host-seeking females of *Ae. cantator* were collected from June 8 through July 12, 1988, at 2 coastal salt marsh habitats in Guilford and Milford, CT. These adults represented the first brood of the year that hatched in early March and began emerging in mid-May. Females were transported to the laboratory and allowed to collectively blood-feed on restrained guinea pigs. Engorged females were individually isolated in 15 × 2.5 × 2.5 cm screened cages and these were placed on wet paper toweling that offered a gradient of moisture for oviposition. Females were supplied with a 10% sucrose solution and held at room temperature (22–24°C, 70% RH) under a natural photoperiod. Oviposition was typically scattered, and the majority of females laid eggs over a 5–7 day period. No attempt was made to offer females a second blood-meal as most died shortly after oviposition. Therefore, each egg batch represented the total egg production from a single female. Eggs from each female were collected daily, counted and transferred to individual 30 ml plastic cups lined with moist filter paper. These eggs were kept moist and held at room temperature (22–24°C) under natural photoperiod (15–14 h light) for 3–4 weeks. Eggs were inundated with 0.3% nutrient broth and larvae hatching from each batch were counted and removed. The hatching medium was withdrawn after 48 h and eggs were thoroughly rinsed in distilled water. Eggs were then transferred to new containers and maintained as described previously until the next flooding. Each egg batch was inundated for a second time on September 1. This date was 3–6 weeks after the first flooding, depending on the egg batch. Eggs and larvae were handled similarly and

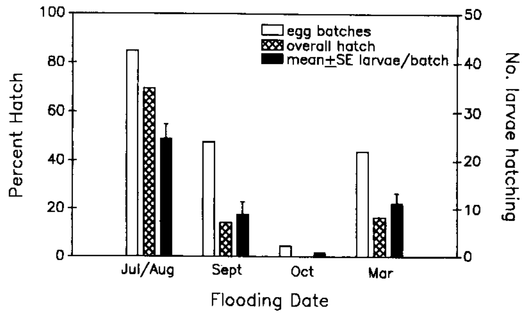

Fig. 1. Hatching response of *Aedes cantator* egg batches with repeated flooding and cold conditioning.

flooded for a third time on October 3. These dates were selected to coincide with natural flooding of the salt marsh habitat. Eggs were then held in the dark on moist filter paper for 5 months at 4°C to simulate winter conditions. Cold conditioned eggs were brought to room temperature and immediately flooded for the last time on March 2, 1989. Records were kept on the number of larvae hatching from each egg batch on each occasion.

Egg production ranged from 342 to 14 eggs per female (batch) and averaged (± SE) 122.0 ± 6.5 (n = 132). Nearly 85% of these egg batches exhibited some hatch in response to the first inundation in July/August (Fig. 1). The mean (± SE) number of larvae hatching from each egg batch was 24.6 ± 2.9 and this represented 69.4% (n = 2,937) of the total overall hatch. Less than half (47.7%) of the egg batches showed some hatch with the second flooding in September, and the mean number of larvae hatching was 8.8 ± 2.6. Very few eggs hatched with the third inundation in October. A total of 6 larvae from 6 egg batches, representing 0.1% of the total hatch was observed.

Almost half (43.9%) of the egg batches displayed some hatch following cold conditioning for 5 months at 4°C. The average number of larvae/egg batch was 11.2 ± 2.1 and this accounted for 16.4% of the total overall hatch. Of the 58 egg batches that hatched in March, 45 (77.6%) of these exhibited some hatch with prior flooding whereas 13 (22.4%) did not. Overall, installment hatching was observed in more than half (56.1%) of the 132 egg batches and roughly one third (34.1%) of these egg batches showed partial hatch both before and after cold conditioning.

Aedes cantator exhibits variable egg hatch in response to serial inundations. Moreover, this behavior appears to primarily result from the production of heterogeneous eggs within a particular batch. This conclusion is based on the observation that although most females of the first generation lay eggs that hatch readily with the first flooding, they also produce others in the same batch that require a second inundation or cold conditioning. This difference in egg hatching represents an important survival strategy for *Ae. cantator* because this mosquito breeds in an unstable environment that is subject to periodic drying and irregular fluctuations. Typical breeding sites, for example, are located on the upland regions of the salt marsh that are not usually replenished by daily high tides (Means 1979). As a result, pools can drain rapidly especially if the marsh is ditched, as most are in the Northeast. In the spring, these sites become heavily flooded following the annual spring tide in March, and with normal rainfall, will usually remain flooded for 9–10 weeks. This extended period of flooding affords ample opportunity for most larvae of the first generation to complete their development. However, in the mid-summer (July–September), these sites become partially flooded with monthly high tides and with warmer weather and less rainfall, can quickly dry up (within 1–2 weeks), often before larvae of subsequent broods can complete their development (Andreadis 1990).

Similar observations have been reported for *Ae. taeniorhynchus*, where installment hatching was attributed to the slow response of a few eggs in most batches as well as a few homogeneous batches (<10%), all of which enter diapause (Moore and Bickley 1966). In the present study, a similarly low percentage (9.8%) of *Ae. cantator* females produced egg batches that required cold conditioning before any eggs would hatch. This observation contrasts sharply with *Ae. sollicitans*, which is reported to readily respond to weak hatching stimuli with a single inundation and produce few diapausing eggs under similar conditions (i.e., long photoperiods) (Travis 1953, Mallack et al. 1964).

It is recognized that the photoperiod and temperature conditions under which juvenile and adult female aedine mosquitoes are subjected to in the maternal generation can have a profound affect on the induction of egg diapause in the following generation (see Danks 1987 for review). Therefore, it is important to emphasize that the present study was conducted with eggs oviposited by first generation *Ae. cantator* and that the hatching response of eggs produced in subsequent broods of this multivoltine species would no doubt differ, most notably in the proportion of eggs undergoing embryonic diapause.

ACKNOWLEDGMENTS

I wish to acknowledge the technical assistance of Kelly Alger, Scott Magnotta and Paul Moore.

REFERENCES CITED

Andreadis, T. G. 1990. Epizootiology of *Amblyospora connecticus* (Microsporida) in field populations of the saltmarsh mosquito, *Aedes cantator*, and the cyclopoid copepod, *Acanthocyclops vernalis*. J. Protozool. 37:174–182.

Becker, N. 1989. Life strategies of mosquitoes as an adaptation to their habits. Bull. Soc. Vector Ecol. 14:6–25.

Breeland, S. G., A. W. Buzicky, E. Pickard and W. I. Barton. 1965. Comparative observations on winter survival and hatching of *Aedes vexans* eggs in two localities—Florence, Alabama, and St. Paul, Minnesota. Mosq. News 25:374–384.

Breeland, S. G. and E. Pickard. 1967. Field observations on 28 broods of floodwater mosquitoes resulting from controlled floodings of a natural habitat in the Tennessee Valley. Mosq. News 27:343–358.

Danks, H. V. 1987. Insect dormancy: an ecological perspective. Biological Survey of Canada Monograph Series No. 1.

Gillett, J. D. 1955a. Variation in the hatching-response of *Aedes* eggs (Diptera: Culicidae). Bull. Entomol. Res. 46:241–254.

Gillett, J. D. 1955b. The inherited basis of variation in the hatching of *Aedes* eggs (Diptera: Culicidae). Bull. Entomol. Res. 46:255–265.

Gjullin, C. M., W. W. Yates and H. H. Stage. 1950. Studies on *Aedes vexans* (Meig.) and *Aedes sticticus* (Meig.), flood-water mosquitoes, in the lower Columbia River Valley. Ann. Entomol. Soc. Am. 43:262–275.

Mallack, J., L. W. Smith, Jr., R. A. Berry, Jr. and W. E. Bickley. 1964. Hatching of eggs of three species of aedine mosquitoes in response to temperature and flooding. Univ. Md. Agric. Exp. Stn. Bull. A-138:1–21.

Means, R. G. 1979. The mosquitoes of New York. Part I. The genus *Aedes* Meigen with identification keys to genera of Culicidae. New York State Mus. Bull. 430a.

Moore, R. C. and W. E. Bickley. 1966. Hatching of the eggs of *Aedes taeniorhynchus* (Weidemann) (Diptera: Culicidae) in response to temperature and flooding. Mosq. News 26:405–415.

Travis, B. V. 1953. Laboratory studies on the hatching of marsh-mosquito eggs. Mosq. News 13:190–198.

Wilson, G. R. and W. R. Horsfall. 1970. Eggs of floodwater mosquitoes. XII. Installment hatching of *Aedes vexans* (Diptera: Culicidae). Ann. Entomol. Soc. Am. 63:1644–1647.

Woodard, D. B., H. C. Chapman and J. J. Petersen. 1968. Laboratory studies on the seasonal hatchability of egg batches of *Aedes sollicitans, A. taeniorhynchus* and *Psorophora confinnis*. Mosq. News. 28:143–146.